

Observations on Chromosomes of *Dicrostonyx torquatus stevensoni* Nelson and Chromosomal Diversity in Varying Lemmings

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Two species of varying lemmings are recognized in North America: the holarctic *Dicrostonyx torquatus* (Pallas) [including *D. groenlandicus* (Traill)], represented by numerous subspecies, and *D. hudsonius* (Pallas), on the Ungava Peninsula of eastern Canada. Since 1962, as animals from different regions could be obtained, we have investigated the chromosomal characteristics of varying lemmings from several geographic populations of *D. torquatus* (Fig. 1). The diploid chromosomal complements of these lemmings have been found to differ among the forms studied, indicating a greater genetic diversity than has been evident from other taxonomic criteria.

In the present report, the somatic chromosomes of *D. torquatus stevensoni* Nelson, from Umnak Island, Alaska, (lat. 53° 15' N; long. 168° 20' W) are described, and the zoogeographic implications of chromosomal differences in varying lemmings are briefly discussed. Findings in other populations will be presented elsewhere.

Materials and Methods

Chromosomes of the following subspecies of *D. torquatus* were studied: *exsul* Allen, from St. Lawrence Island (Bering Sea); *nelsoni* Merriam, from the Seward Peninsula (near Nome); *richardsoni* Merriam, from the western shore of Hudson Bay (near Churchill, Manitoba, Canada); *rubricatus* (Richardson), from the central arctic coast of Alaska (Point Barrow), the northeastern arctic coast of Alaska (Beaufort Lagoon), and the central Brooks Range (near Anaktuvuk Pass); and *stevensoni* Nelson, from Umnak Island (Aleutian Islands). Breeding colonies of all forms except *D. t. exsul* were established in the laboratory, and numerous crosses between animals from the different populations were made.

The colony of *D. t. stevensoni* was established with 3 males and 4 females captured on Umnak Island by Dr. F. H. FAY during August 1958. The animals studied were taken from the colony over a period of years (2 in 1963, 2 in 1964, 7 in 1966, 1 in 1967, 11 in 1968, 1 in 1969, 2 in 1970, 6 in 1971, and 5 in 1972). When examination of the earlier preparations was undertaken in late 1968, it was determined that chromosomal polymorphism existed among the captive animals. Since 1968, tissues of animals studied have included marrow from all, spleen from all but one, lung from 4, skin from 3, testes from 5, and ovaries from 3. Preparations of chromosomes from bone marrow, spleen, and testes were made by standard methods using acetic orcein stain; from testes with lactic-acetic orcein (WELSHONS et al. 1962); and from ovaries *in vitro* (HENDERSON and EDWARDS 1968) without definitive results. Lung and skin were cultured in flasks by methods described earlier (FAY et al. 1967), and cells were prepared for examination according to the recommendations of Hsu (1969), but with an increased amount of Colcemid (1 µg/ml); trypsin was used to free the cellular monolayer.

Karyotypes, with pairs grouped by size and according to position of the centromere (median, submedian, or terminal regions), were prepared by inspection from 17 animals; those from 7 males and 7 females were assembled after measurements (see LEVAN et al. 1964) indicated presumed homologues.

Autoradiographic studies using tritiated thymidine were made on lung cells in tissue-culture from 6 animals in order to identify the allocyclic X-chromosome, following methods described by SCHMID (1965) and ÁRNASON (1970). Sex-chromatin was examined in cells from

the external root-sheath of vibrissae (SCHMID 1967); only the chromocenter clearly adjacent to the cell membrane was counted as indicating a positive result. The relative size of the X and Y chromosomes was determined from linear measurements and is given as a percentage of the total length of the haploid complement.

Results

From each of 14 males and 22 females of *D. t. stevensoni*, 10 to 60 cells were examined. In a total of 802 cells, 79.5% contained 34 chromosomes; the modal number in males was 34 (32 + XY), and in females 34. Of the 22 females, 9 (40%) were found to have an apparent deletion in one X-chromosome; following the notation of BIANCHI and CONTRERAS (1967) and BIANCHI et al. (1971) for South American akodont rodents, the two types of females are designated 32XX and 32Xx, the latter indicating the deletion.

Karyotypes of one male and two females are shown in Figs. 2–4. No variation was seen in karyotypes of males, the autosomes of which included 5 pairs with centromeres in the median region (arm ratio 1.0–1.58; av. 1.22), 4 pairs, one very small, with submedian centromeres (arm ratio 1.43–3.10; av. 2.06), 6 pairs with sub-



Fig. 1. Map of Alaska and adjacent regions, showing localities from which varying lemmings were obtained, and general distribution of subspecies of *D. torquatus*

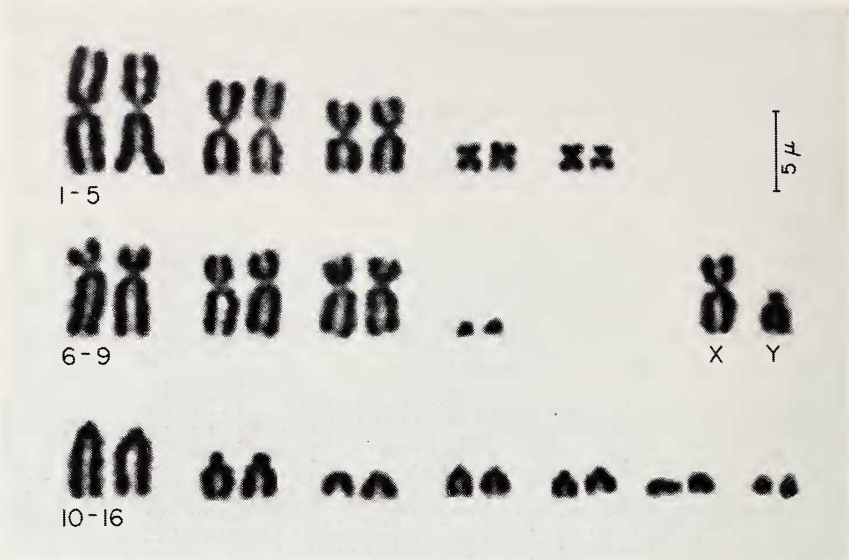


Fig. 2. Karyotype of *D. t. stevensoni*, male

terminal centromeres (arm ratio 2.58–12.5; av. 4.98), and 1 pair with the centromere in the terminal region (pair No. 10, arm ratio 10.69–22.11; av. 15.63). The centromere in the probable X-chromosome was submedian (arm ratio 1.12–1.70; av. 1.49), and that in the Y-chromosome, subterminal (arm ratio 2.11–5.15; av. 3.31). The designated Y-chromosome was similar to those of pair No. 11, but in every cell was easily distinguishable by its shorter total length and the less terminal position of the centromere. The length of the relatively large Y ranged from 3.9–5.3 % (av. 4.3 %)

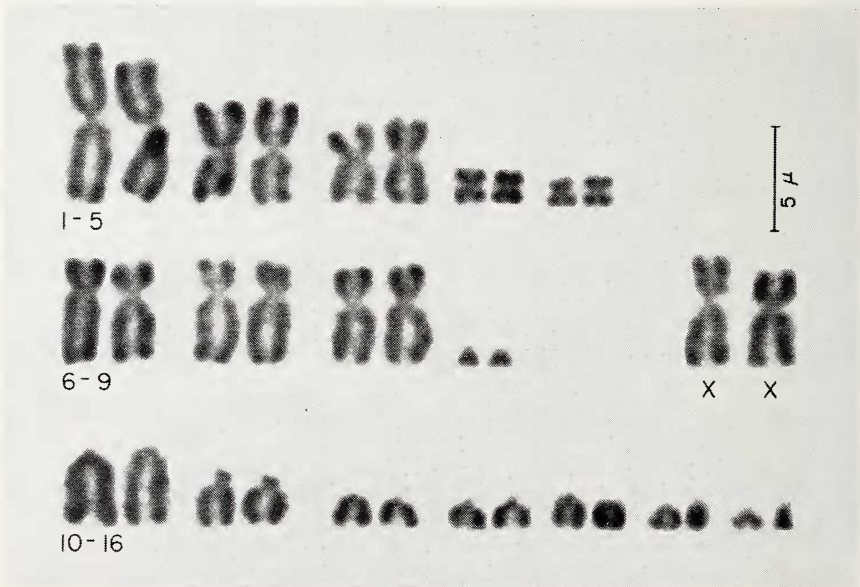


Fig. 3. Karyotype of *D. t. stevensoni*, female (32XX)

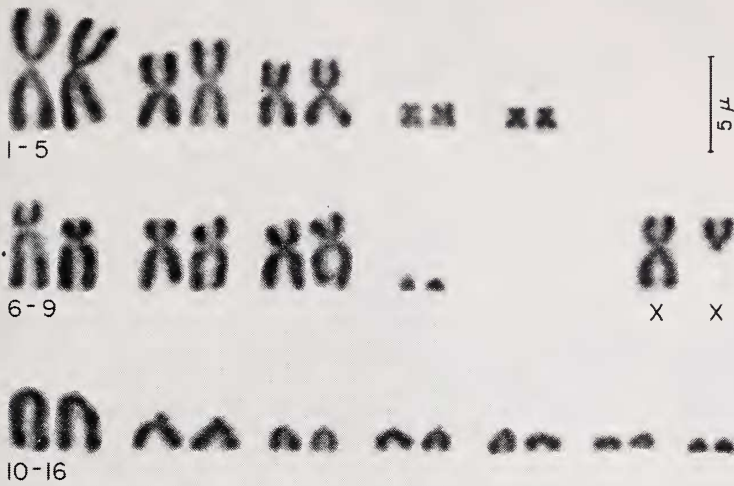


Fig. 4. Karyotype of *D. t. stevensoni*, female, with partial deletion in one X-chromosome (32XX)

of the male haploid set. In meiotic preparations from males, 16 autosomal bivalents plus X and Y were evident, the sex chromosomes associating end-to-end (Fig. 5).

In karyotypes of females, the autosomes were similar to those of males. In females with a diploid complement of 32XX, the position of the centromere (Fig. 3) in both designated X-chromosomes was submedian (arm ratio 1.15–1.72; av. 1.62). In females with 32Xx, the greater portion of the long arm of one X-chromosome was absent (Fig. 4); the range of arm ratio of the deleted X-chromosome was 2.61–3.50, with an average of 2.93. The length of the remaining (long) arm of the deleted X was found consistently to be similar to that of the short arm of the undeleted X. Fragments were not found in any cells. In autoradiography, the pattern of DNA-replication in females (32XX) showed the heaviest concentration of grains on one submedian chromosome, the measurements and arm ratio of which fell within the range of those of the X-chromosome, and we interpreted this element to be the asynchronous X. Only indirect evidence of the replication pattern was seen for females with 32Xx; in two F₁ female offspring of *D. t. stevensoni* x *D. t. exsul*, the heaviest labelling involved one element that morphologically was like the deleted X-chromosome. Karyotypes of such offspring were very similar to those of the parent stock from Umnak Island.

The undeleted X-chromosome of *D. t. stevensoni* was found to be larger than the original-type X of mammals described by OHNO et al. (1964 et seq.). Its length in both types of females ranged from 8.26–10.4% (av. 8.75%) of the genome. In females with 32Xx, the length of the deleted X comprised 3.45–4.45% (av. 3.8%) of the haploid set.

The NF (fundamental number; MATTHEY 1945, et seq.) of *D. t. stevensoni* was found to be 54.

Discussion

Dicrostonyx unalascensis stevensoni, described by NELSON (1929) from 14 specimens collected on Umnak Island during the months of November and December, was distinguished by large size and cranial characteristics. NELSON also noted that this

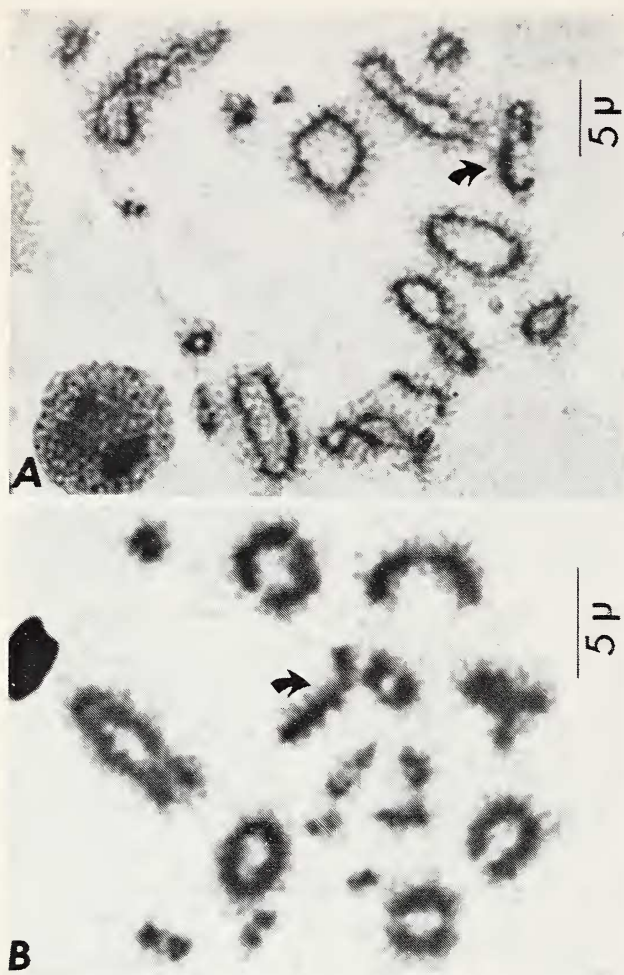


Fig. 5. Meiotic preparations (A = diplotené, B = diakinetik) from male *D. t. stevensoni*. Sex chromosomes are indicated by arrows. (Testis squash, acetic orcein stain)

form of varying lemming did not molt to a white winter pelage. *D. unalascensis stevensoni* was considered to be a subspecies of *D. groenlandicus* by HALL and COCKRUM (1953).

The taxonomic discriminants distinguishing this form also include cytogenetic characters. Although a basic chromosomal complement appeared to be common to all populations of *Dicrostonyx* that we sampled, our studies of lemmings from Umnak Island and preliminary comparisons with those from other areas (see map, Fig. 1) indicated that Robertsonian rearrangements, deletions or possibly pericentric inversions in some somatic chromosomes have taken

place in all these forms. These modifications will be described in subsequent reports.

The deleted X occurred in a significant proportion of females (9 of the 22 studied: 40%) in the captive colony of *D. t. stevensoni*. Such females were fertile and produced fertile young, some litters of which included females with complements of either 32XX or 32Xx. We did not find females with the deleted X from 32XX females, nor did we find any males that had the deletion. It seemed probable that such males, if indeed zygotes of the combination 32xY were formed, did not survive to birth, and there was some indication that females with the deletion produced a lower than normal proportion of male offspring. Mosaicism in the females has not been excluded as a possibility, but seems unlikely. In somatic tissues, the enumeration of cells with other than the diploid number of 34 was not greater than that in 32XX females or in males, and the deleted X was present consistently. Two females with 32Xx and 5 with 32XX were examined for sex chromatin, and the former were found to be negative. Of 176 to 320 cells counted from each of the 5 positive animals, one sex-chromatin body, approximately $1.4 \times 0.7 \mu$ in size, was present in 50.2 to 79%. Studies of oöcytes, so far unproductive except that they indicated a haploid number of 17, and of oögonia we hope will resolve this question.

The undeleted X-chromosome of *D. t. stevensoni* is possibly of the "duplicate-type" (OHNO et al. 1964), since its size is near 10% of the female haploid complement. The pattern of H³-thymidine labelling seen, with granular concentration only or most heavily on the long arm of the late-replicating X, suggests that such arms are largely heterochromatic and are later in synthesizing DNA than the shorter arms which are relatively euchromatic and in synchrony with the autosomes, such as was cited by OHNO (1967) to be the case for certain other mammals. The heterochromatic regions may make up that portion that has been lost in some females. The Y-chromosome is comparatively large (about 4.3% of the haploid constitution), a finding that seems compatible with the designation of the X as being of the duplicate-type. Those males (4) studied for sex-chromatin were negative, and only one chromocenter was identified in sex-chromatin-positive females.

Observations on the laboratory colonies of varying lemmings suggest that the deleted X-chromosome might be a factor in the population dynamics of *D. t. stevensoni* and other forms of *D. torquatus* known to possess the character. In natural populations, if some females have ova with the deleted X, their breeding would bring about a change in the sex ratio, but productivity presumably would be increased; at times of low numerical density, a disproportionately small number of males might reduce the probability of breeding and tend to suppress productivity. For South American akodont rodents, which seem similar to *Dicrostonyx* in cytogenetic characteristics, BIANCHI et al. (1971) suggested that the X-deletion, as a form of dosage compensation, occurs partially or completely in somatic cells only, that germinal cells do not produce ova with a deleted X, and that no xY males are produced. BIANCHI and his coworkers did not detect disproportionate sex ratios in the natural populations of *Akodon* spp. that they sampled, nor have we found indications from the literature or from personal observations in Alaska of unbalanced sex ratios in natural populations of varying lemmings.

Since the laboratory colonies of *Dicrostonyx* and other arvicoline rodents were maintained primarily to supply experimental animals for use in the investigation of zoonotic diseases, we did not record data on reproduction that would have been useful in the present study. Numbers of young born were listed routinely, but the sex often was not determined for animals dying at birth or soon thereafter. Pairs of varying lemmings were maintained only as long as they were prolific, and then replaced with younger, more productive animals. The following data with these deficiencies are for 13 pairs of *D. t. stevensoni* selected at random from the colony. The gestation period was usually 21 days, although occasionally the first litter was born on the 20th day. The 13 pairs produced a total of 95 litters, with 327 young. The number of litters from each pair ranged from 3 to 12, with an average of 7. For 4 pairs that produced a total of 39 litters (12, 10, 10, 7), the interval between births of litters ranged from 21 to 94 days, with an average of 31 days and a mode of 22–23 days. The intervals between litters usually began to increase after the 5th or 6th. For the 95 litters, numbers of young ranged from 1 to 7 (av. 3.4 per litter), with a distribution as follows: 14 litters of 1; 18 of 2; 17 of 3; 17 of 4; 17 of 5; 11 of 6; and 1 litter of 7.

In the laboratory, where the respective colonies consisted of relatively few individuals, unbalanced sex ratios (most often a scarcity of males) at times caused difficulties in maintaining the stocks. In one series of 213 young produced by the colony of *D. t. stevensoni*, 123 were females and 90 (42%) were males. A similar observation was reported by MANNING (1954), who found that only 31% of 119 laboratory-reared varying lemmings were males. MANNING stated (p. 45) that "It is tentatively suggested that one or more of the small number of feral lemming contributing to the colony may have had an inheritable tendency to produce more than the normal

proportion of females." The lemmings in MANNING's colony were derived from two populations, *groenlandicus* and *kilangmiutak*. It is conceivable that the interbreeding of mixed stock resulted in an unbalanced sex ratio, as was seen in our experimental cross-breeding of individuals from the respective populations.

In cross-breeding involving *D. t. stevensoni*, the results were as follows, with numbers of progeny indicated: *stevensoni* x *exsul*, 4 ♂♂ and 7 ♀♀; *stevensoni* x *nelsoni*, 16 ♂♂ and 16 ♀♀; *stevensoni* x *richardsoni*, 5 ♂♂ and 35 ♀♀; *stevensoni* x *rubricatus*, 3 ♂♂ and 4 ♀♀. In all cases, attempts were made to breed the F₁ progeny, but none produced young.

The F₁ progeny of the aforementioned crosses were also crossed back to parent forms: (*stevensoni* x *exsul*) x *stevensoni*, 12 ♂♂ and 32 ♀♀ produced (sex was not recorded for 21 additional young discarded soon after birth); (*stevensoni* x *richardsoni*) x *richardsoni*, 1 ♂ and 2 ♀♀; (*stevensoni* x *rubricatus*) x *rubricatus*, 3 ♀♀. Some other crosses also were made, including progeny of the back-cross (*stevensoni* x *exsul*) x *stevensoni*, which produced 20 ♂♂, 35 ♀♀, and 4 for which sex was not recorded. Other findings in the progeny of these crosses will be reported elsewhere.

That greater numbers of females were produced in most of the experiments does not necessarily indicate the influence of the deleted X-chromosome. It suggests, also, that the heterogametic sex in *Dicrostonyx* may suffer from deficiencies introduced by hybridization (see CRAFT 1938), and that some of the geographically isolated populations of varying lemmings are genetically quite divergent, for which some indications are provided by zoogeographic data as well.

Zoogeographic Considerations

According to present taxonomic concepts, *Dicrostonyx torquatus* is a polytypic species of circumpolar distribution. In Eurasia, it inhabits the tundra from the Mezen' River in the west to the Bering Sea coast of the Chukchi Peninsula in the east. Four Eurasian subspecies are recognized: *torquatus* (Pallas) and *chionopaes* Allen, on the mainland; and *ungulatus* (von Baer) and *vinogradovi* Ognev, on Novaia Zemlia and Wrangell Island, respectively (OGNEV 1948, GROMOV et al. 1963). In summer pelage, *D. t. torquatus* appears to be nearly indistinguishable from *D. t. nelsoni*, from the Seward Peninsula of Alaska. *D. t. chionopaes* is more brightly colored, resembling *D. t. rubricatus*, from the arctic coast of Alaska. The karyologic characteristics of Eurasian forms of *D. torquatus* have not been defined.

Varying lemmings occur extensively in arctic and subarctic North America, on many of the islands of the Canadian Arctic Archipelago, and in northern Greenland. Twelve North American subspecies of *D. torquatus* are recognized: *clarus* Handley, *exsul* Allen, *groenlandicus* (Traill), *kilangmiutak* Anderson and Rand, *lentus* Handley, *nelsoni* Merriam, *nunatakensis* Youngman, *peninsulae* Handley, *richardsoni* Merriam, *rubricatus* (Richardson), *stevensoni* Nelson, and *unalascensis* Merriam. The most recently described, *nunatakensis*, is known only from the Ogilvie Mountains, in Yukon Territory, Canada (YOUNGMAN 1967). The distribution of the other nearctic forms is shown by HALL and KELSON (1959 map, p. 766). A second nearctic species, *Dicrostonyx hudsonius*, occurs on the Ungava Peninsula, east of Hudson Bay.

The presence of *D. torquatus* in deposits of Riss age in northeastern Siberia (VANGENGEIM 1961) lends support to the hypothesis that varying lemmings occupied the Amphiberingian refugium during the penultimate glaciation (HOPKINS 1967, fig. 2), with subsequent dispersal eastward during the Riss/Würm interglacial. REPENNING (1967) concluded that *Dicrostonyx* entered North America during early Rancholabrean (pre-Würm) time, as indicated by the finding of remains of *D. hudsonius* in Pleistocene deposits in Pennsylvania (GUILDAY and DOUTT 1961). Remains

of *D. torquatus* also were found in cave-deposits of late-Pleistocene age in Wyoming (GUILDAY 1968). Evidence for its occurrence in the periglacial tundra during Würm time invalidates the earlier hypothesis that *D. torquatus* spread only from the Amphiberingian region during post-glacial time (GUILDAY 1963, RAUSCH 1963). In the most recent review of the zoogeography of varying lemmings in North America, GUILDAY (1968) suggested two hypotheses to account for the recent distribution of *D. torquatus* and *D. hudsonius*: 1. that the zone of periglacial tundra was discontinuous, with the two forms separated in eastern and western areas; 2. that the periglacial tundra was continuous and was occupied by varying lemmings that showed a clinal variation in dental pattern from west to east. In either case, with recession of the continental glacier, the eastern form occupied the region east of Hudson Bay.

The complex distributional history of *D. torquatus*, as indicated by the fossil remains and by the range of genetic diversity observed by us, appears to be compatible with the hypothesis proposed by MACPHERSON (1965): Having occupied suitable habitat during pre-Würm time, populations of varying lemmings became fragmented or displaced southward during Würm time, with relict stocks persisting in unglaciated refugia and in periglacial tundra. The known distribution of ice-free tundra during the glacial maximum of Würm time has been shown by MACPHERSON (1965, fig. 2). Post-glacial dispersal of populations of diverse origins resulted in a reoccupation of suitable habitat.

Although lemmings of the *torquatus*-group are morphologically quite uniform, some subgroups may be distinguishable. MACPHERSON (1965 p. 161) noted that "... a distinct complex of races occupies Greenland and the high Arctic and extends deeply into the central archipelago. This group, I assume, must have arisen from a stock isolated in Pearyland . . .", and that "The western mainland and Baffin Island races appear to represent a related group of Beringian origin, except for *D. t. richardsoni*, which may have had a southern origin."

In the western Arctic, HALL and KELSON (1959) recognized 5 subspecies of *D. groenlandicus* (= *D. torquatus*) in Alaska and on adjacent islands. The sixth taxon, *D. t. exsul*, was considered to be specifically distinct. On the Alaskan mainland, varying lemmings inhabit the zone of arctic tundra in the north and west, as well as subarctic treeless regions to the southwest, including the Alaska Peninsula. The distribution of these subspecies in continental North America is usually considered to be continuous, with contiguity between ranges of subspecies (cf. HALL and KELSON 1959, map 427). However, recent vegetational maps as well as personal observations indicate that habitat of varying lemmings is discontinuous, and there are no records of intergradation of nominal subspecies in Alaska. To the east, the forested valley of the lower Mackenzie River appears to separate *D. t. rubricatus* from *D. t. kilangmiutak* (ANDERSON and RAND 1945; MANNING and MACPHERSON 1958). The distribution of these two forms suggests that they were derived from separate relict populations.

The populations of varying lemmings that were studied exhibited a range of chromosomal polymorphism, in which differences existed in number and morphology of chromosomes, as well as in fundamental number. In addition to partial deletion of the X-chromosome in some females (in at least *exsul*, *nelsoni*, and *stevensoni*), other modifications in presumed X-chromosomes were observed. Numbers of chromosomes and fundamental numbers of the respective forms are summarized in Table 1.

Of the 4 nominal subspecies of *D. torquatus* studied in Alaska, *stevensoni* and *exsul* had the same number of somatic chromosomes and of major chromosomal arms. However, their chromosomes differed morphologically, and the mating of F₁ progeny of *stevensoni* x *exsul* was not productive. The two populations probably have been long isolated geographically.

Table 1
Some karyotypic characters of populations of varying lemmings

Subspecies	Geographic Origin	Chromosomes		
		2n (Somata)		NF
		♂	♀	
<i>exsul</i>	St. Lawrence Island	?	34	54
<i>nelsoni</i>	Seward Peninsula	30	30	54
<i>richardsoni</i>	Churchill, Canada	42, 44	42	50
<i>rubricatus</i>	Anaktuvuk Pass	35	34	54
	Beaufort Lagoon	33	32	55
	Point Barrow	33	33	54
<i>stevensoni</i>	Umnak Island	34	34	54

During the glacial maximum of Würm time, Umnak Island formed the southwesternmost limit of the exposed Bering-Chukchi platform, beyond which migration of terrestrial mammals was prevented by Samalga Pass to the west (Fig. 1). Umnak and Unalaska Islands, as well as Unimak Island and the Alaska Peninsula, were largely glacier-covered, but probably had ice-free areas representing the southern limits of the Amphiberingian refugium (KARLSTROM 1961; LINDROTH 1963, fig. 6). That the Recent mammalian faunas of Umnak (varying lemming only) and Unalaska (varying lemming and *Microtus oeconomus* [Pallas]) are depauperate suggests that these areas were formerly habitable only by species highly adapted to arctic conditions. *M. oeconomus*, which apparently had an extensive distribution within the refugium, might have become established on Unalaska more recently.

D. t. stevensoni and *D. t. unalascensis* may be the most closely related of the peripheral isolates, since gene flow could hardly have been obstructed during the last glaciation by the narrow valley that is now Umnak Pass. As NELSON (1929) observed, *stevensoni* does not acquire a white pelage in winter, and such appears to be the case also for *unalascensis* (GILMORE 1933). This characteristic seems to be a secondary adaptation in populations isolated in a subarctic region of relatively mild, maritime climate with intermittent snow-cover in winter. To confirm that *stevensoni* does not molt to a white winter pelage, we placed a male *stevensoni*, a female *rubricatus* (stock from Point Barrow), and one each male and female F₁ progeny of *stevensoni* x *rubricatus* in outdoor cages at Anchorage, Alaska, on 5 September 1960. The *rubricatus* and the two F₁ crosses acquired white pelage and snow-claws, but the winter pelage of the male *stevensoni* was only slightly paler than that of summer, and there was in this animal no indication of the formation of snow-claws. The experiment was repeated, with the same results. The inheritance of this characteristic has not been investigated further. *Stevensoni* and evidently *unalascensis* are unique among varying lemmings in the possession of this trait.

St. Lawrence Island, where *D. t. exsul* occurs, was a part of the Beringian refugium during the Riss and Würm glaciations and was the last of the islands in the Bering Sea to be isolated by rising sea-level at the end of Würm time (HOPKINS 1959). The terrestrial mammalian fauna of the island now consists of 5 species [not including *Alopex lagopus* (Linnaeus) and other carnivores that may move actively or passively on sea-ice], all of which have differentiated infraspecifically from corresponding forms on the Siberian and Alaskan mainlands (RAUSCH 1953). *D. t. exsul* inhabits high, relatively dry, rocky areas with heath-lichen vegetation, and does not characteristically occur in the wet tundra of the lowlands, which is occupied by *Microtus oeconomus*. Conceivably, competitive interactions between *M. oeconomus* and *D. t. exsul* also may tend to restrict the latter to the alpine biotope (F. H. FAY, unpublished data; also see MORRIS and GRANT 1972).

We know nothing of the chromosomes of *D. t. peninsulae*, occurring on Unimak Island and perhaps on the Alaska Peninsula. The varying lemmings in that southern region may be derivatives of one or more local isolates, or of post-glacial immigrants from the northeast. Both Unimak Island and the peninsula have continental faunas as a result of post-glacial immigration.

D. t. nelsoni, found on the Seward Peninsula and in the areas adjacent to the south, has four less chromosomes than *stevensoni* and *exsul*, but also a fundamental number of 54. F₁ progeny of *nelsoni* x *exsul* were fertile. While we consider infertility in F₁ progeny from crosses between animals representing two nominal subspecies to be significant evidence of divergence, we cannot yet rank the fertility of such offspring from *nelsoni* x *exsul* as indicating a degree of relationship greater than that existing among the other forms studied.

The varying lemmings of northern Alaska, ostensibly referable to *rubricatus*, are uniform in some phenotypic characters, but some chromosomal elements varied among the three populations studied. In reference to the population in the Brooks Range, BEE and HALL (1956 p. 61) observed that those animals possibly differed infra-specifically. We found that crosses between individuals from Point Barrow and Anaktuvuk Pass produced fertile progeny, and intergression appeared to be complete in the laboratory colony. Cross-breeding involving animals from Beaufort Lagoon has not been attempted.

D. t. richardsoni, with 42—44 somatic chromosomes in most of which the centromeres were subterminal, and a fundamental number of 50, differed markedly from varying lemmings in Alaska. MACPHERSON (1965) tentatively postulated a southern origin for *richardsoni*. MATTHEY (1965) reported 44 as the normal diploid complement for 2 males of *D. groenlandicus*, for which the exact geographic origin in Canada was not known (MATTHEY, personal communication). He also observed 42 chromosomes in some of his preparations, but considered such constitutions to be aberrant.

In the laboratory, the crossing of varying lemmings representing combinations of nominal subspecies was uniformly successful. However, with the single exception noted (*exsul* x *nelsoni*), the mating of the respective F₁ progeny was not productive. Preliminary examination of sections of testes and ovaries from some of these animals indicated that male sterility may be frequent. No significant ethological differences were noted in making the respective crosses; when a male and a female representing two subspecies were placed together, copulation occurred as promptly as with two individuals of the same stock. The F₁ progeny of all derivatives also mated readily, but produced no offspring.

Comparisons of the chromosomes of insular and mainland populations of rodents of other species considered to have been inhabitants of the Beringian refugium during Würm time revealed no recognizable differences in most cases, in contrast to findings in varying lemmings. Such comparisons included *Lemmus sibiricus* Kerr from St. George Island (Pribilof Islands) and Point Barrow; *Microtus oeconomus* from St. Lawrence Island, Amak Island (Bering Sea, at the tip of the Alaska Peninsula), and the Kenai Peninsula (south-central Alaska); *Microtus abbreviatus* Miller (? = *M. miurus abbreviatus*) from St. Matthew Island (Bering Sea) and *M. miurus* Osgood from Umiat (north-central Alaska) (RAUSCH and RAUSCH 1968, and unpublished). A slight difference in certain chromosomes was noted in *Clethrionomys rutilus* (Pallas) from St. Lawrence Island, yet individuals of the insular form successfully interbred with animals from the vicinity of Anchorage (south-central Alaska). All of the aforementioned crosses made in the laboratory were found to be indefinitely fertile. Some of the insular populations differ from their mainland counterparts in other phenotypic characters to a greater degree than any of the populations of *Dicrostonyx torquatus* (except *stevensoni*) differ from one another.

Other lines of evidence sometimes support inferences concerning the temporal sequence of faunal interchanges. The occurrence of host-specific endoparasites (helminths: VON IHERING 1902) and of fleats (Siphonaptera; HOLLAND 1963) provides indications of the distributional histories of their hosts.

Two species of nematodes, *Heligmosomoides hudsoni* (Cameron, 1937) and *Syphacia arctica* Tiner and Rauch, 1950, are host-specific parasites inhabiting the cecum of varying lemmings, the former always found tightly coiled around the specialized cecal villi. *H. hudsoni* was described from *Dicrostonyx hudsonius*; it apparently occurs also in lemmings on Baffin Island, and we have recorded it from Beaufort Lagoon, Anaktuvuk Pass, and Umnak Island in Alaska. *S. arctica* is known from animals from Point Barrow and Anaktuvuk Pass. In Eurasia, *H. hudsoni* has been reported from varying lemmings on Wrangell Island by NADTOCHII (1970), who also found *Syphacia* sp. in 9 of the 10 examined. A consideration of the distribution of *H. hudsoni* suggests that it entered North America with the precursor of the Recent forms of *Dicrostonyx* (including *D. hudsonius*) and persisted in various isolated populations during the Würm glaciation. *Andrya arctica* Rausch, 1952 is the common cestode of varying lemmings in arctic Alaska, and has been reported also in animals from Churchill, Manitoba, and from Prince Patrick Island in the Canadian Arctic Archipelago. It is not known to occur in Eurasia. Its lack of host-specificity obscures its possible significance as a zoogeographic indicator. The characteristic flea of varying lemmings in North America is the nearctic *Megabothris groenlandicus* (Wahlgren). Holarctic species of mammals of Amphiberingian origin (e. g., *Citellus parryi*, *Clethrionomys rutilus*, *Microtus oeconomus*) typically harbor holarctic species of fleas (HOLLAND 1963).

The findings reported here support the proposition that *Dicrostonyx* became widely distributed in arctic North America before Würm time, during which populations survived in refugia and in periglacial tundra. While manifesting a high degree of developmental homeostasis, some of these geographic isolates have undergone chromosomal reorganization with genotypic change to the extent that the taxa studied (*exsul*, *nelsoni*, *richardsoni*, *rubricatus*, and *stevensoni*) evidently are reproductively isolated as well. By these criteria, the "torquatus-group" in North America appears to be a superspecies.

The relationships of the varying lemmings will be better understood after chromosomal characteristics have been defined for all the nearctic forms and for those in Eurasia. Further genetic investigations would be of great interest as well. The varying lemmings, easily maintained in the laboratory, would seem suitable as a model for the study of polymorphism in sex chromosomes.

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Summary

The cytogenetic characteristics of the varying lemming, *Dicrostonyx torquatus stevensoni*, ($2n = 34$), were investigated, and diploid chromosomal numbers were reported for four other nominal subspecies (*exsul*, *nelsoni*, *richardsoni*, and *rubricatus*) of the *torquatus*-group in North America. The diploid complements ranged from 30 to 44 chromosomes, and the fundamental number from 50 to 55. Chromosomal polymorphism was observed in all forms. In cross-breeding experiments, the mating of F_1 progeny was not productive. The findings support the zoogeographic concept that populations of *Dicrostonyx* became fragmented or displaced southward during Würm time, with relict stocks persisting in unglaciated refugia or periglacial tundra. Speciation in the isolates led to chromosomal evolution, with the result that populations spreading from refugia in post-glacial time are reproductively isolated. The *torquatus*-group in North America appears to be a super-species.

Zusammenfassung

*Untersuchungen an den Chromosomen von Dicrostonyx torquatus stevensoni
Nelson und chromosomale Unterschiede bei Halsbandlemmingen*

Die cytogenetischen Merkmale des Halsbandlemmings, *Dicrostonyx torquatus stevensoni*, ($2n = 34$) wurden eingehend untersucht, und für vier andere nordamerikanische Unterarten der *torquatus*-Gruppe wurden die somatischen Chromosomensätze festgestellt. Die Chromosomenzahl der untersuchten Populationen schwankte zwischen 30 und 44, der NF (Nombre Fundamental) zwischen 50 und 55. Zuchttiere der verschiedenen Populationen wurden erfolgreich gekreuzt, aber Sterilität der F_1 Unterartbastarde war typisch. Die Halsbandlemminge wiesen Karyotypenverschiedenheiten auf, die sich durch Variationen des Robertsonschen Typus, Deletionen oder möglicherweise durch perizentrische Inversionen erklären. Die Ergebnisse sprechen dafür, daß das ursprüngliche Verbreitungsgebiet von *Dicrostonyx* in Nordamerika durch die letzte (Würm) Vereisung getrennt wurde, und daß die Reliktpopulationen die letzte Glazial-Phase in eisfreien Refugien oder in periglazialer Tundra überlebten, wo Karyotypevolution durch lokale Anpassungsbedürfnisse gefördert wurde. Die in der Postglazialzeit aus den Refugien sich verbreitenden Populationen von *Dicrostonyx* scheinen reproduktiv isoliert zu sein. Die *torquatus*-Gruppe in Nordamerika gilt also als Superspecies.

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